Cyclically competing species: deterministic trajectories and stochastic evolution

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Content

- Cyclic dominance of competing species: real-world examples
- Predation and exchange rates
- The well-mixed situation: spaceless model
  - Mean field results: deterministic trajetories
  - Stochastic evolution: extinction events
- Coarsening and coexistence in one dimension
- Coarsening in two dimensions

Acknowledgement

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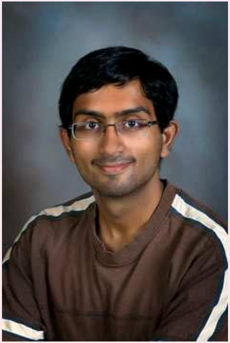
Siddharth Venkat

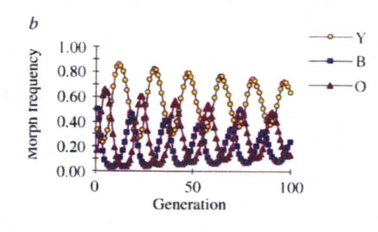


Clinton Durney, Sara Case, Royce Zia

David Konrad, Ahmed Roman

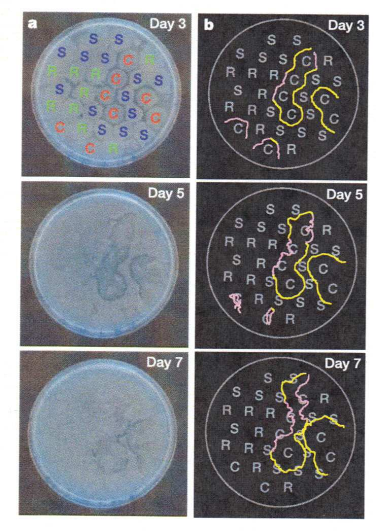
Cyclic dominance of competing species

real-world example: lizard populations in southern California (Sinervo/Lively '96)



Cyclic dominance of competing species

real-world example: competing bacterial strains (*Escherichia coli*) (Kerr et al. '02)



Rock-Paper-Scissors game

three cyclically competing species: Rock-Paper-Scissors game

$$\begin{aligned} a + b &\xrightarrow{k_a} a + a \\ b + c &\xrightarrow{k_b} b + b \\ c + a &\xrightarrow{k_c} c + c \end{aligned}$$

three ways of realizing mobility when on a lattice:

- exchange of individuals

$$\begin{aligned} a + b &\overset{s_{ab}}{\rightleftarrows} b + a \\ b + c &\overset{s_{bc}}{\rightleftarrows} c + b \\ c + a &\overset{s_{ca}}{\rightleftarrows} a + c \end{aligned}$$

  conserved quantity: $N_a + N_b + N_c = N$

- empty sites
- multiple occupancy of sites

Four species model

$$
\begin{aligned}
a + b &\xrightarrow{k_a} a + a \\
b + c &\xrightarrow{k_b} b + b \\
c + d &\xrightarrow{k_c} c + c \\
d + a &\xrightarrow{k_d} d + d
\end{aligned}
$$

mobility on the lattice: exchange of individuals

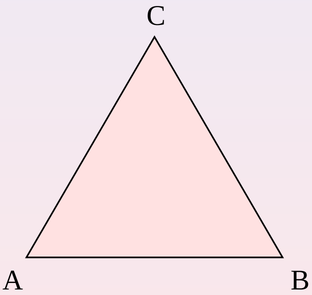
$$
\begin{aligned}
a + b &\overset{s_{ab}}{\rightleftarrows} b + a \\
b + c &\overset{s_{bc}}{\rightleftarrows} c + b \\
c + d &\overset{s_{ca}}{\rightleftarrows} d + c \\
d + a &\overset{s_{ca}}{\rightleftarrows} a + d
\end{aligned}
$$

conserved quantity: $N_a + N_b + N_c + N_d = N$

formation of partner-pairs!

Well-mixed system

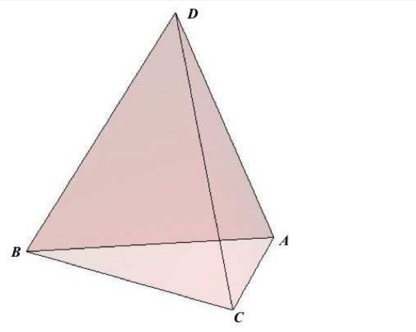
configuration space for three species



three absorbing states

Well-mixed system

configuration space for four species



ac and *bd* pairs do not interact

$\Longrightarrow$ final (absorbing) state displays coexistence of these pairs

every point along $a - c$ and $b - d$ edges represents such a state
$\Longrightarrow 2(N + 1)$ absorbing states

Well-mixed system

mean field approximation for the evolution of the averages of the fractions

$$A(t) \equiv \sum_{\{N_m\}} (N_a/N)\, P(\{N_m\}\,;t) \quad \text{etc.}$$

neglect all correlations and replace averages of products by the products of averages

MF equations ($k_a + k_b + k_c + k_d = 1$):

$$\begin{aligned}
\partial_t A &= [k_a B - k_d D]\, A \\
\partial_t B &= [k_b C - k_a A]\, B \\
\partial_t C &= [k_c D - k_b B]\, C \\
\partial_t D &= [k_d A - k_c C]\, D
\end{aligned}$$

Well-mixed system

mean field approximation for the evolution of the averages of the fractions

$$A(t) \equiv \sum_{\{N_m\}} (N_a/N)\, P\left(\{N_m\}\,;\,t\right) \quad \text{etc.}$$

neglect all correlations and replace averages of products by the products of averages

MF equations ($k_a + k_b + k_c + k_d = 1$):

$$\begin{aligned}
\partial_t \ln A &= k_a B - k_d D \\
\partial_t \ln B &= k_b C - k_a A \\
\partial_t \ln C &= k_c D - k_b B \\
\partial_t \ln D &= k_d A - k_c C
\end{aligned}$$

Well-mixed system

contributions from a single species to the growth/decay of two other species:

$$\begin{aligned}\partial_t \left[k_b \ln A + k_a \ln C\right] &= \lambda D \\ \partial_t \left[k_c \ln A + k_d \ln C\right] &= \lambda B \\ \partial_t \left[k_c \ln B + k_b \ln D\right] &= -\lambda A \\ \partial_t \left[k_d \ln B + k_a \ln D\right] &= -\lambda C\end{aligned}$$

key control parameter: $\lambda \equiv k_a k_c - k_b k_d$

quantity

$$Q \equiv \frac{A^{k_b+k_c} C^{k_d+k_a}}{B^{k_c+k_d} D^{k_a+k_b}}$$

evolves in an extremely simple manner:

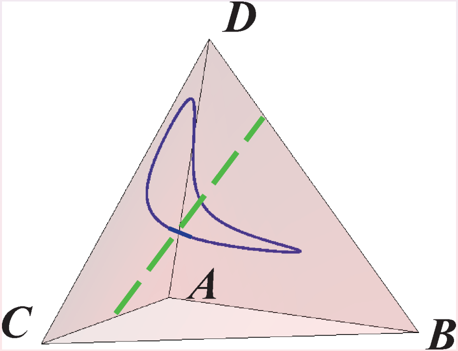
$$Q(t) = Q(0)\, e^{\lambda t}$$

Well-mixed system

$\lambda = 0 \longrightarrow k_a k_c = k_b k_d$

Q is a constant of motion

saddle-shaped orbits and fixed points

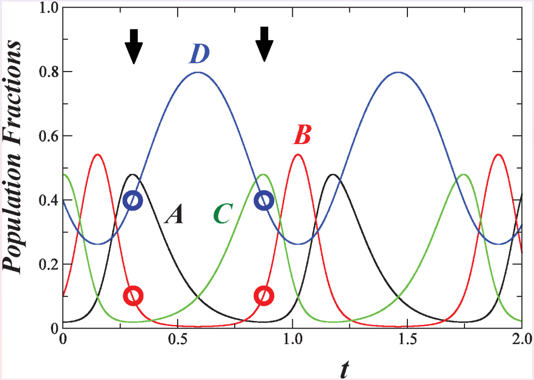


$(k_a, k_b, k_c, k_d) = (0.4, 0.4, 0.1, 0.1)$ and
$(A_0, B_0, C_0, D_0) = (0.02, 0.10, 0.48, 0.40)$

Well-mixed system

$\lambda = 0 \longrightarrow k_a k_c = k_b k_d$

Q is a constant of motion



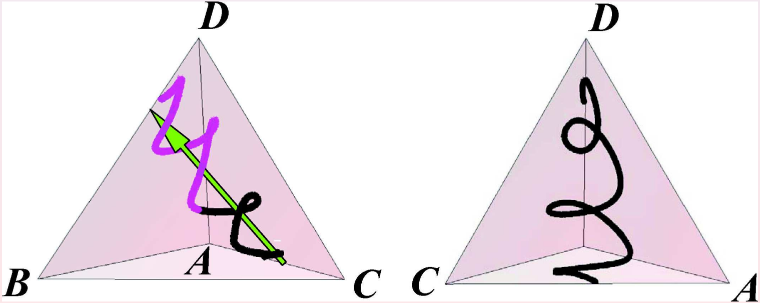
$(k_a, k_b, k_c, k_d) = (0.4, 0.4, 0.1, 0.1)$ and
$(A_0, B_0, C_0, D_0) = (0.02, 0.10, 0.48, 0.40)$

Well-mixed system

$\lambda \neq 0$

$$Q(t) = Q(0)\, e^{\lambda t} \quad \text{with} \quad Q \equiv \frac{A^{k_b+k_c} C^{k_d+k_a}}{B^{k_c+k_d} D^{k_a+k_b}}$$

spirals and arrows

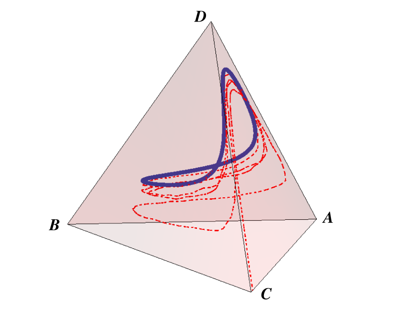


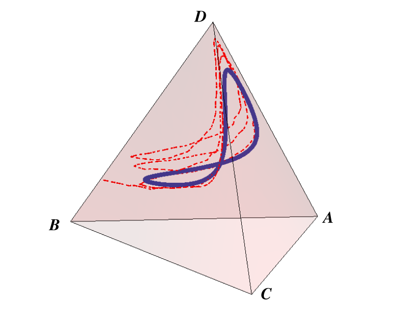
starting from symmetry point with $\lambda = -0.0273$

Well-mixed system

going beyond mean field approximation: numerical simulations

$\lambda = 0$: stochastic effects



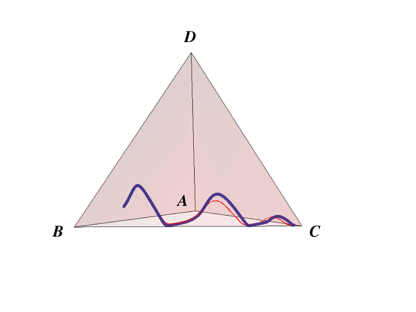


1000 particles, $(k_a, k_b, k_c, k_d) = (0.4, 0.4, 0.1, 0.1)$ and $(A_0, B_0, C_0, D_0) = (0.02, 0.10, 0.48, 0.40)$

Well-mixed system

going beyond mean field approximation: numerical simulations

$\lambda \neq 0$: extinction events

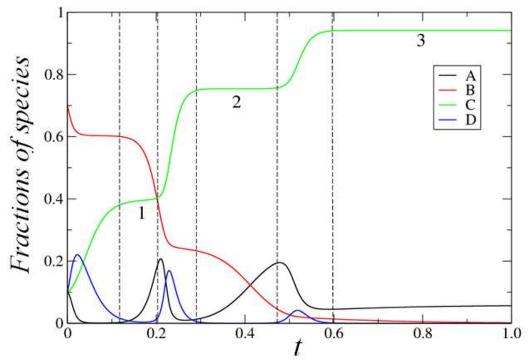


$(k_a, k_b, k_c, k_d) = (0.1, 0.0001, 0.1, 0.7999)$ and
$(A_0, B_0, C_0, D_0) = (0.1, 0.7, 0.1, 0.1)$

Well-mixed system

going beyond mean field approximation: numerical simulations

$\lambda \neq 0$: extinction events

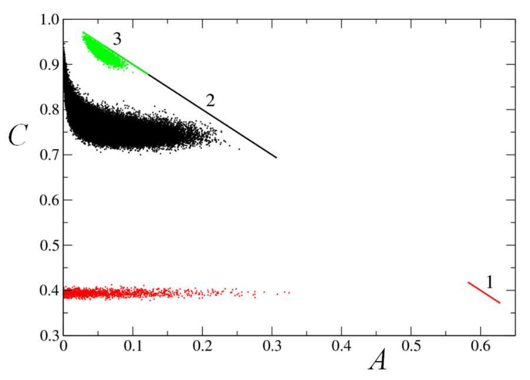


$(k_a, k_b, k_c, k_d) = (0.1, 0.0001, 0.1, 0.7999)$ and
$(A_0, B_0, C_0, D_0) = (0.1, 0.7, 0.1, 0.1)$

Well-mixed system

going beyond mean field approximation: numerical simulations

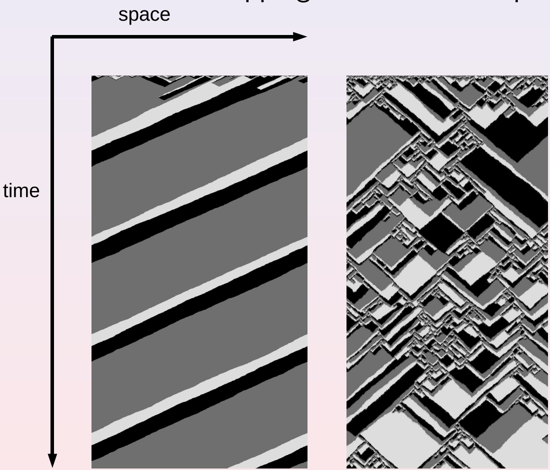
$\lambda \neq 0$: extinction events



$(k_a, k_b, k_c, k_d) = (0.1, 0.0001, 0.1, 0.7999)$ and
$(A_0, B_0, C_0, D_0) = (0.1, 0.7, 0.1, 0.1)$

Coarsening and coexistence in one dimension

Symmetric interaction and swapping rates for three species

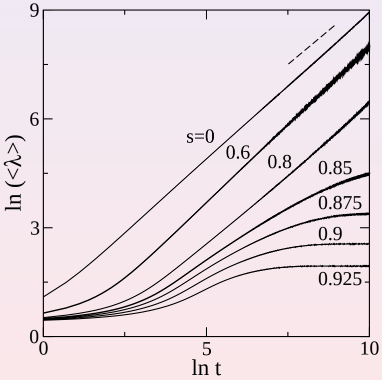


$k = 0.9, \; s = 0.1$ $\qquad$ $k = 0.1, \; s = 0.9$

Coarsening and coexistence in one dimension

Symmetric interaction and swapping rates for three species

average domain size (for $k + s = 1$)

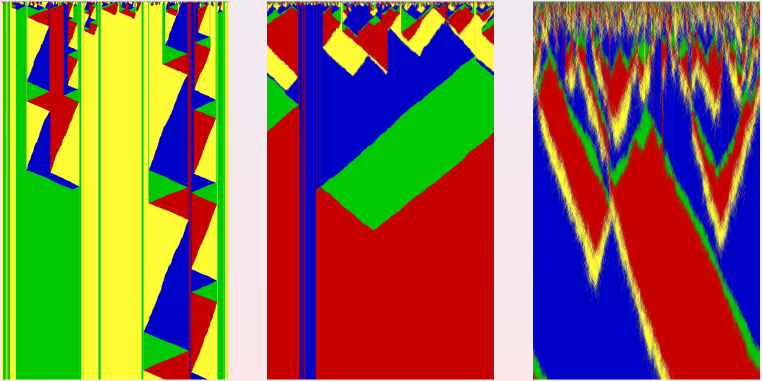


swapping rates s larger than $s_c \approx 0.84$:
exchange mechanism very effectively mixes different species
$\longrightarrow$ coexistence of species is promoted

Coarsening and coexistence in one dimension

Symmetric interaction and swapping rates for four species

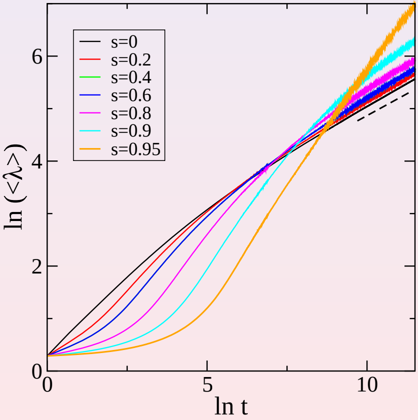
space-time diagrams



$k = 0.8,\ s = 0.2$ $k = 0.1,\ s = 0.9$ $k = 0.01,\ s = 0.99$

Coarsening and coexistence in one dimension

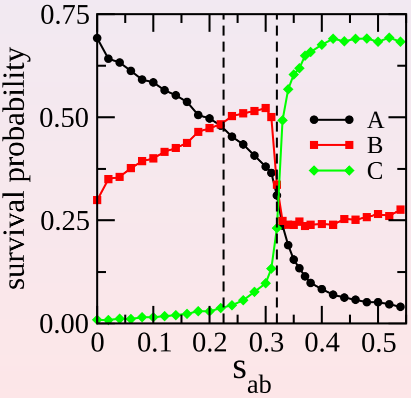
Symmetric interaction and swapping rates for four species
average domain size (for $k + s = 1$)



$\longrightarrow$ exchanges speed up the coarsening process!

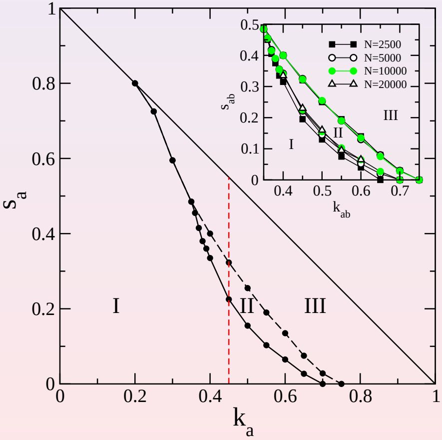
Asymmetric interaction and swapping rates for three species
asymmetry in the rates $\Longrightarrow$ dominance of a single species

Example: $k_a = 0.45,\ k_b = k_c = 0.4,\ s_{bc} = s_{ca} = 0.4$



Coarsening and coexistence in one dimension

Asymmetric interaction and swapping rates for three species dynamical phase diagram for $k_b = k_c = 0.4$, $s_{bc} = s_{ca} = 0.4$



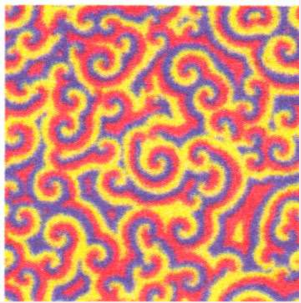
I: A dominates, II: B dominates, III: C dominates

Coarsening in two dimensions

three species

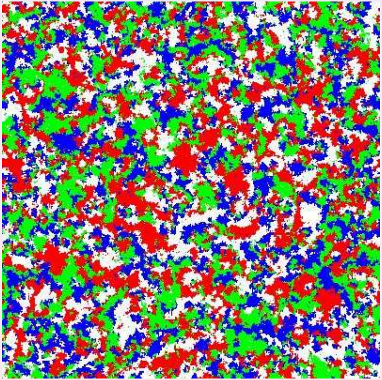
May-Leonard model with swapping of particles (Reichenbach '07)

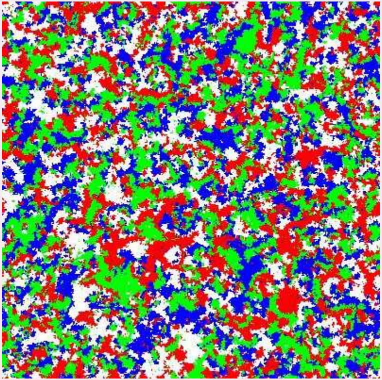
$A + B \longrightarrow A + 0,\ A + 0 \longrightarrow A + A,\ A + B \longrightarrow B + A$ etc.



Coarsening in two dimensions

four species: coexitence, but no well formed space-time patterns



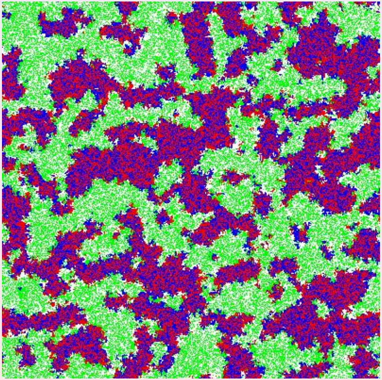


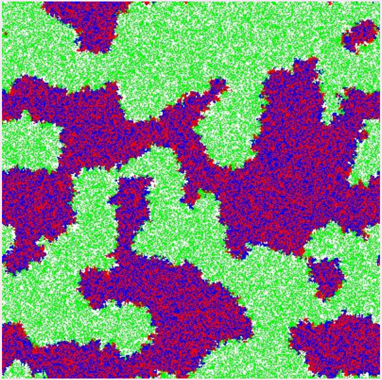
$k = 1$ and $s = 0$

Coarsening in two dimensions

four species with exchanges between individuals belonging to a partner-pair

$\Longrightarrow$ coarsening of partner-pair domains





$k = 1$ and $s = 0$, $s_{pp} = 1$

Conclusion

Cyclic competition between three and four species

- well-mixed system with four species

  key control parameter: $\lambda \equiv k_a k_c - k_b k_d$

  mean-field approximation: trajectories shaped like saddles, spirals, arrows
  stochastic effects: different extinction scenarios

- three and four species on a ring

  different effects due to mobility
  three species: high mobility yields coexistence
  four species: high mobility speeds up coarsening

- four species in the plane

  coarsening of partner-pair domains when allowing exchanges of partners

References

S. Venkat and M. Pleimling
Phys. Rev. E **81**, 021917 (2010)

S. O. Case, C. H. Durney, M. Pleimling, and R. K. P. Zia
EPL **92**, 58003 (2010)

C. H. Durney, S. O. Case, M. Pleimling, and R. K. P. Zia
Phys. Rev. E **83**, 051108 (2011)

Cyclic dominance of competing species

other examples:

- self-organizing Min proteins (Loose et al. '08)
- coral reef invertebrates (Buss/Jackson '79)
- endogeneous and exogeneous origins of diseases modeled as a four-species model (Sornette '09)
- invading grass species (complicated competition between five species) (Silvertown et al. '92)